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ADVANTAGES AND RESTRICTIONS IN THE USE OF POSTCRANIAL SKELETON IN PHYLOGENETICAL ANALISYS: THE EXAMPLE OF THE "CONDYLARTHRA" OF THE SÃO JOSÉ DE ITABORAÍ BASIN [1]

(With 2 figures)

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ABSTRACT: The importance of the postcranial skeleton in understanding the affinities of ungulates has been recognized since the turn of the Twentieth Century, but its use in phylogeny is still limited because some authors underestimate the informative content of postcranial bones.

In spite of the small number of phylogenetic studies employing postcranial characters, some significant examples are found in the literature about the contribution of the postcranial skeleton in the recognition of the affinities of mammals. Among those is *Victorlemoinea prototypica* ("Condylarthra", Sparnotheriodontidae), from the São José de Itaboraí Basin, Rio de Janeiro, Brazil (Itaboraian). *V. prototypica* was originally included in the order Litopterna based on its dental features. The study of its tarsal morphology revealed the absence of the typical tarsal specializations of that order. *V. prototypica* was then transferred to the order "Condylarthra ". Other bones of the skeleton corroborated its position in this order.

Using the software PAUP 3.1 and 153 postcranial characters, a phylogenetic analysis of the "Condylarthra" and hoofed South American mammals was undertaken. In all attempts, *Victorlemoinea* was grouped with *Lamegoia* and *Paulacoutoia* ("Condylarthra", Didolodontidae) and the Litopterna formed a monophyletic group that was well defined on postcranial bones. However, the resulting topology of the analysis including all taxa also reflected a locomotor-dependent arrangement, and the clades represented evolutionary degrees related to a greater or lesser capacity for terrestrial locomotion.

The postcranial skeleton is very informative and contributes to enlarge the understanding of the affinities among taxa. However, as it is more subjected to homoplasies than the cranium and teeth, in analyses involving taxa of different orders, the use of postcranial characters exclusively can fail in revealing the real relationship among the groups, tending to group forms with similar habits. The postcranial morphology has larger aplicability in the establishment of the affinities among taxa of the same order.

Key words: Phylogeny, "Condylarthra", Litopterna, skeleton, São José de Itaboraí Basin, Paleocene.

RESUMO: Vantagens e restrições na utilização do esqueleto pós-craniano em análise filogenética: o exemplo dos "condylarthra" da Bacia de São José de Itaboraí.

Desde o início do século XX a importância do esqueleto pós-craniano no entendimento das afinidades entre os ungulados é reconhecida, mas sua utilização na filogenia dos mamíferos ainda é pequena, pois alguns autores subestimam o conteúdo informativo dos ossos pós-cranianos.

Apesar do pequeno número, alguns exemplos significativos são encontrados na literatura sobre a contribuição do esqueleto pós-craniano no reconhecimento das afinidades dos mamíferos. Dentre esses, destaca-se o de *Victorlemoinea prototypica* ("Condylarthra", Sparnotheriodontidae), da Bacia de São José de Itaboraí, Rio de Janeiro/Brasil (Itaboraiense). *V. prototypica* foi originalmente incluída na ordem Litopterna, por sua morfologia dentária, mas o conhecimento da morfologia tarsal revelou a inexistência das especializações típicas da ordem, sendo transferida para a ordem "Condylarthra". Outros ossos do esqueleto corroboraram seu posicionamento nessa ordem.

Utilizando o programa PAUP 3.1 e somente caracteres pós-cranianos (153) foi realizada uma análise filogenética de todos os "Condylarthra" e ungulados sul-americanos. Em todas as tentativas, *Victorlemoinea* foi agrupada com *Lamegoia* e *Paulacoutoia* ("Condylarthra", Didolodontidae), enquanto os Litopterna formaram um grupo monofilético bem definido por caracteres pós-cranianos. Entretanto, a topografia resultante da análise conjunta de todos os táxons também refletiu um arranjo locomotor-dependente, tendo os clados representado graus evolutivos relacionados a maior ou menor capacidade de locomoção terrestre.

O esqueleto pós-craniano é muito informativo e contribui para o maior esclarecimento das afinidades entre táxons. Entretanto, por ser mais sujeito a homoplasias que o crânio e dentes, em análises envolvendo táxons de diferentes ordens, a inclusão apenas de caracteres pós-cranianos pode falhar em revelar as reais afinidades entres os grupos, tendendo a agrupar formas com hábitos similares. A morfologia pós-craniana tem maior aplicabilidade no estabelecimento das afinidades entre táxons de uma mesma ordem.

Palavras-chave: Filogenia, "Condylarthra", Litopterna, esqueleto, Bacia de São José de Itaboraí, Paleoceno.

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INTRODUCTION

The importance of the postcranial skeleton in understanding the affinities among ungulates has been recognized since the turn of the Twentieth Century, (*e.g.* MATTHEW, 1909). However, its use in the phylogeny of mammals has been limited. Some authors still underestimate the informative content of the postcranial bones, giving them brief descriptions beside extensive descriptions of cranial and dental morphology.

SZALAY (1977:369) explained the restricted use of postcranials in mammal phylogeny with the following statement: "Most past studies of eutherian phylogenetic relationships which considered both fossil and extant taxa heavily favored cranial and dental evidence. Besides the greater abundance of fossil dentitions, the major reason for overlooking bone morphology in favor of teeth is believed to be based on a mistaken view of ontogeny and phylogeny. It's widely and erroneously held by paleomammalogists that because bone is sometimes ontogenetically more plastic than teeth, it is phylogenetically more prone to change and therefore convergence. This view ignores the fact that evolutionary modification is the result of change in gene frequencies and not of ontogenetic transformation of occasional individuals."

In spite of the small number, some significant examples of the contribution of postcranial skeleton in the recognition of mammals affinities are found in the literature. According to MATTHEW (1909), while only the teeth morphology was well known, the origin of Artiodactyla and Perissodactyla were easily related to "Condylarthra". The study of the postcranial skeleton showed that, by the lower Eocene (Wasatch beds), the astragalus of the Artiodactyla and Perissodactyla had already been differentiated as in the derived forms, suggesting no close relationship with "condylarths".

A similar example is known for primates. Gaudry (*apud* MATTHEW, 1909) hypothesized that primates were related to "condylarths" based on dental morphology. The study of the postcranial skeleton revealed that the special features observed in primates' hands and feet were not found among "condylarths" (MATTHEW, 1909).

Based on the presence of prominent upper tusks, bilophodont teeth and inflated nasal area, *Pyrotherium* Ameghino, 1888 (Pyrotheria, Pyrotheriidae) was related to Proboscidea, but a better knowledge of its anatomy refuted this conception (PATTERSON & PASCUAL, 1972).

More recently, ROSE (1987) reinforced the importance of the postcranial skeleton in the understanding of the ancestry of Artiodactyla. After studying the postcranial bones of *Chriacus* Cope, 1883 ("Condylarthra", Arctocyonidae), he concluded that the supposed ancestry of the order Artiodactyla from this genus, based on its dental morphology, was incompatible with the specializations observed in the postcranial skeleton that completely diverges from the adaptations developed by Artiodactyla.

CIFELLI (1983), CIFELLI & GUERRERO-DIAZ (1989), CIFELLI & VILLARROEL (1997) showed that the study of the postcranial skeleton can lead to more significant changes in previously established concepts. Due to the presence of postcranial characters shared only by litoptern species, these authors transferred *Megadolodus* McKenna, 1975, *Prothoatherium* Ameghino, 1902, *Miguelsoria* Cifelli, 1983 and *Protolipterna* Cifelli, 1983 to the order Litopterna, in spite of their primitive dental morphology that is very similar to the members of the order "Condylarthra".

As shown above, the postcranial skeleton has an important role in the understanding of mammalian relationships. This contribution reinforces this importance and points out the restrictions of its use on the basis of the study of some ungulate fossils of Itaboraí Basin (Rio de Janeiro, Brazil, Upper Paleocene).

DISCUSSION

Victorlemoinea prototypica Paula-Couto, 1952 was originally assigned to the order Litopterna, family Macraucheniidae, based on its markedly selenolophodont dental morphology (PAULA-COUTO, 1952; see also SIMPSON, 1948). Like all other Itaboraí taxa but *Carodnia* Simpson, 1935, *V. prototypica* is known only by its dental morphology. CIFELLI (1983), working with isolated tarsal bones from the Itaboraí Basin, assigned a group of large condylarth-like calcanea and astragali to *V. prototypica*. The absence of any litoptern ankle specializations in these bones, such as the relative posterior position of the astragalocalcaneal facets on the calcaneum, astragalar body spool-shaped and absence of superior astragalar foramen, led CIFELLI (1983)

to remove *V. prototypica* from the order Litopterna and place it in the order Condylarthra, family Sparnotheriodontidae. He also considered it's tooth morphology "...aberrantly specialized in some respects and far more derived than the most primitive undoubted members of the family [Macrauchenidae], the Cramaucheniinae...". *V. prototypica* would be a precociously specialized relative of the litoptern, that was convergent upon them (CIFELLI, 1983:25). A combining of advanced teeth and a primitive postcranial skeleton is also present in the North American *Meniscotherium* Cope, 1874 (WILLIANSON & LUCAS, 1992).

BERGQVIST (1996) reevaluated CIFELLI´s (1983) assignment of primitive anklebones to *V.* prototypica. His proposal was not only corroborated but other bones of primitive morphology were also assigned to the species. She also did a series of phylogenetic analysis based exclusively on postcranial characteres, using the software Paup 3.1 and 153 potentially informative characters. In all the resulted topographies *Victorlemoinea* emerged as a close related taxon of the condylarths *Lamegoia* Paula-Couto, 1952 and *Paulacoutoia* Cifelli, 1983, and the litoptern members were grouped in a monophyletic assemblage (Fig.1-C12 and Fig.2-C11).

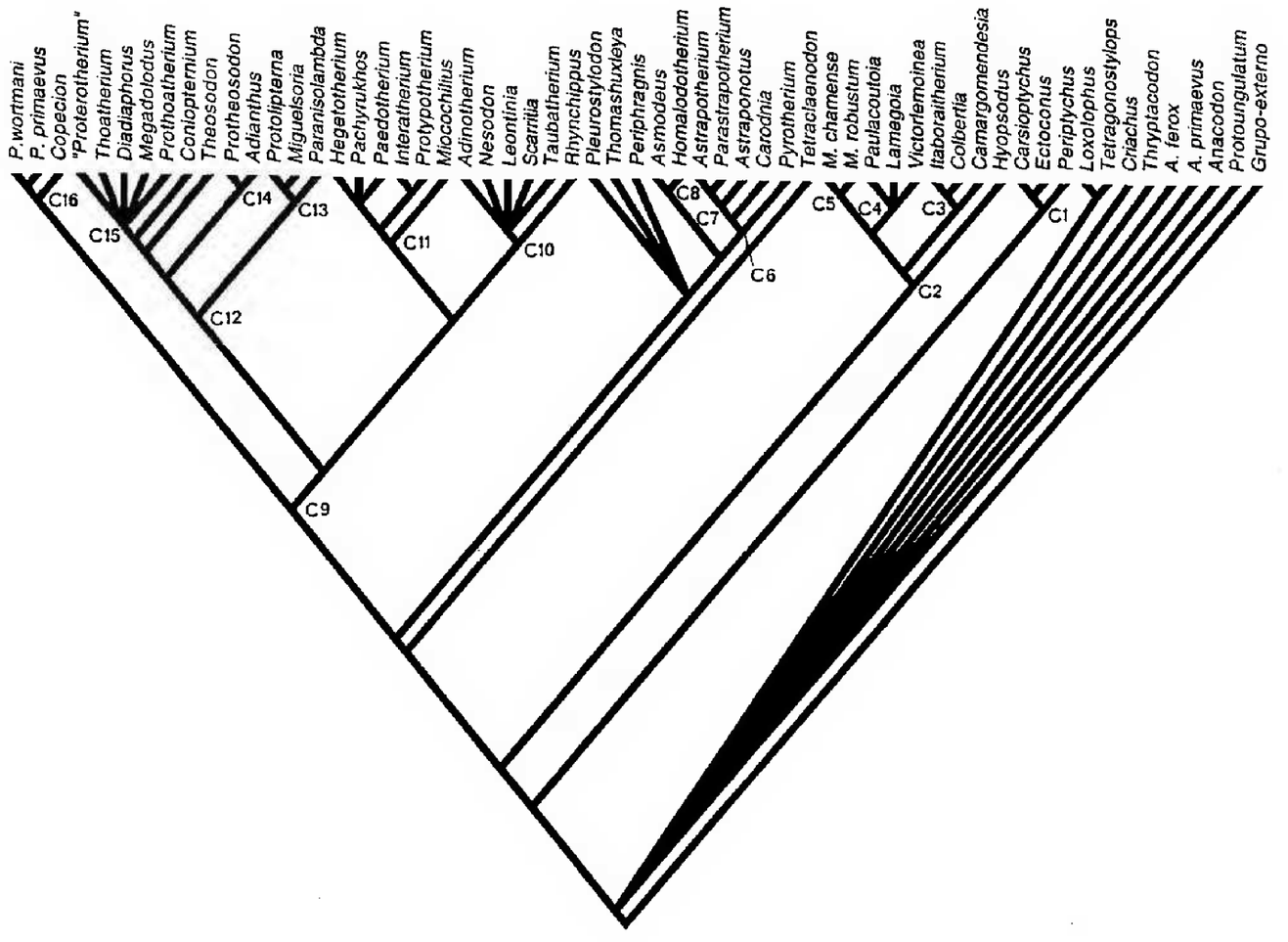

Fig.1- Strict consensous cladrogram resulting from the phylogenetic analysis of North American "condylarths" and South American ungulates, using PAUP (BERGQVIST, 1996).

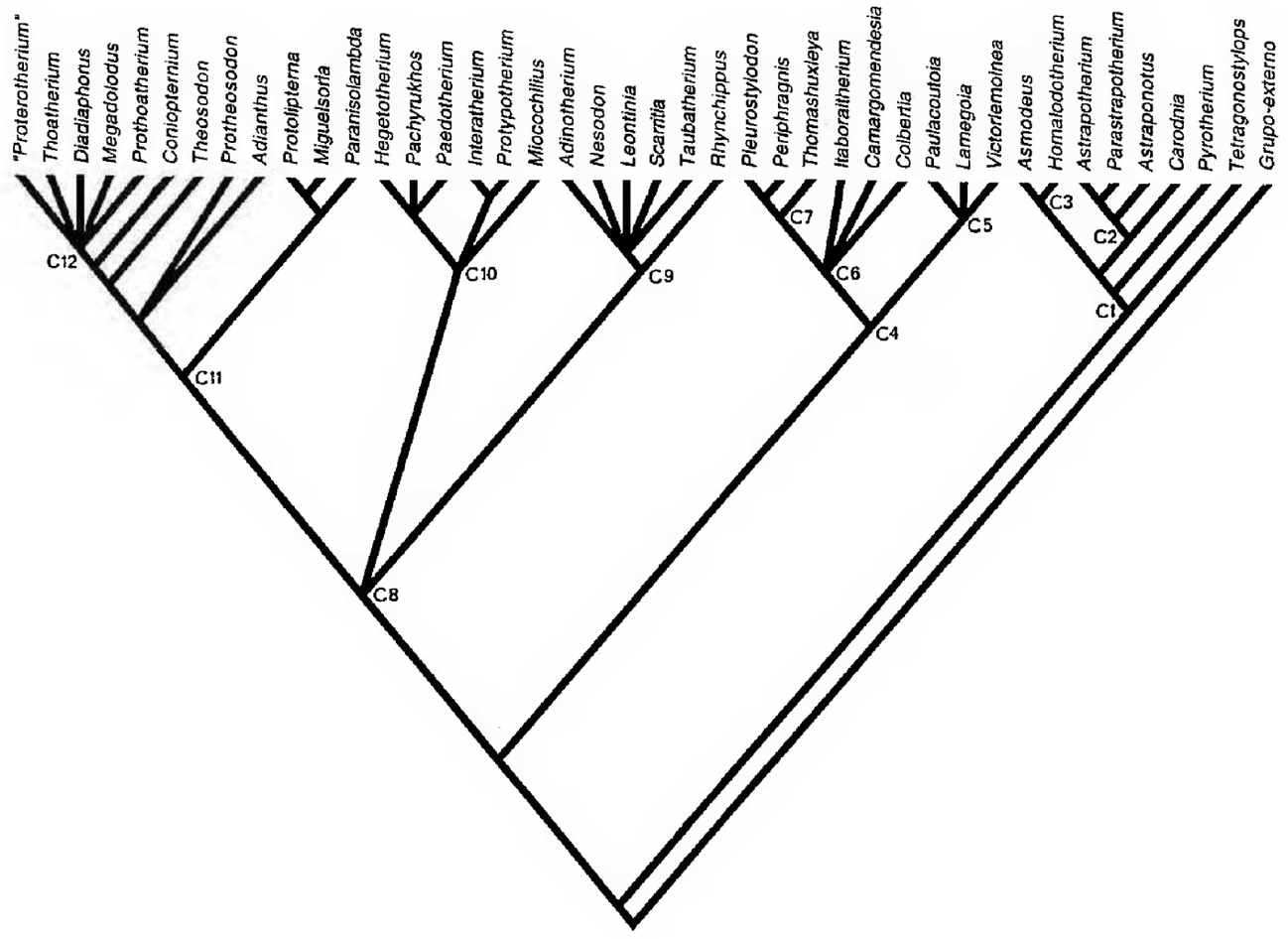

Fig.2- Strict consensous cladrogram resulting from the phylogenetic analysis of South American ungulates, using PAUP (BERGQVIST, 1996).

Nevertheless, the topography of the cladogram of figure 1 also showed a notably locomotor-dependent arrangement, with clades representing evolutionary degrees related to a major or minor capacity of terrestrial locomotion (*e.g.* the grouping of *Phenacodus* Cope, 1881 and *Copecion* Gingerich, 1989 the more cursorial North American condylarths, with litoptern and more cursorial notoungulates [Fig.1-C9]). Nonetheless, the litoptern members were always grouped in a monophyletic assemblage, showing the consistence and well establishment of the order.

The use of postcranial characters in phylogenetic analysis, as shown above, is undoubtedly important, but like any other anatomical system, it presents difficulties and restrictions. According to SZALAY & DAGOSTO (1980) the problems reside in the narrow relationship between the proportions of the skeleton and morphology of the long bones, with the locomotion way or habit of the animal. ROSE & EMRY (1993) illustrated this observation with the comparison of the humerus of *Priodontes* Cuvier, 1827 (Cingulata) and *Vombatus* Saint-Hilaire,1803 (Marsupialia), pointing out the notable degree of homoplasy between them. This way, structural similarity can result from similarities in function, not simply proximity of relationship, and the groups that present such structures won't constitute a monophyletic unit (CRACRAFT, 1981).

CONCLUSIONS

A well-supported hypothesis of *Victorlemoinea* affinities with the condylarths, and the consistency of the monophyletic nature of the

litopterns were revealed when postcranial characters were used in the phylogenetic analysis, calling the attention to the importance of the considerations of postcranial characters in fossil mammal phylogenies.

The postcranial skeleton is very informative and contributes to enlarge the understanding of the affinities among mammal taxa. However, as most of the time it is more subjected of homoplasies than skull and teeth, in analyses involving taxa of different orders, the use of postcranial characters exclusively can fail in revealing the real relationship among the groups, tending to group forms with similar habits. The postcranial morphology has larger applicability in the establishment of the affinities among taxa of the same order.

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